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TWO SPECIES OF TORTOISES IN NORTHERN SOUTH AMERICA

By Ernest E. Williams

In 1825 Thomas Bell beautifully figured and clearly distinguished two species of land tortoise from northern South America. His plates (later reproduced in Sowerby and Lear) give an excellent idea of most of the characters by which they are even now to be distinguished. Yet 130 odd years later the two forms are still customarily synonymized, though occasional (not fully documented) suggestions that they may be distinct have been made (e.g., Luederwalt, 1926).

I was first led into the study of this problem when, during my work on a fossil Cuban tortoise, I was struck by the variability of the position of the gular-humeral sulcus in relation to the entoplastron in American Museum specimens of "*Testudo denticulata.*" At that time (1950, p. 14) I published a mention of this remarkable (as I then thought) intraspecific variability. However, during my visits to European museums during tenure of a Guggenheim Fellowship in 1952-53, I became aware that two forms, each defined by several correlated characters, were being confused under the names "*denticulata*" or "*tabulata,*" used synonymously, but I was not then sure whether subspecies or species were involved. I have since examined all northern South American tortoises in the Museum of Comparative Zoology (MCZ), the American Museum of Natural History (AMNH), the Chicago Natural History Museum (CNHM), the Philadelphia Academy of Natural Sciences (PANS), and the United States National Museum (USNM), as well as those of the Departamento de Zoologia (DZ), São Paulo, Brasil. It has become evident that the two forms are in several places sympatric or nearly so and that they are best interpreted as two species — the same two species distinguished by Bell in 1825.

The species are not difficult to separate and are not in any genuine sense siblings, despite some tendency to overlapping variability. Variability tending to produce overlaps in individual characters is characteristic of all closely related species of turtles — that is, of all forms which have not at some time been separated generically. In this case as in others of this sort, recognition of species is never to be made on any single supposed key character but on the balance of characters in the character complex. If determination of species is made on total characters, no individual should be at all doubtful or difficult to place.

I present below in parallel columns the differences which seem to me useful in diagnosing the two species.

denticulata	*carbonaria*
Adult dorsal shell brown, nearly uniform or with vaguely bounded lighter areolae — juveniles nearly uniform yellow brown	Adult dorsal shell black, usually with small sharply bounded yellow areolae—juveniles like adults black and yellow
Prefrontal scales elongate	Prefrontal scales short
Frontal scale usually broken up	Frontal scale usually entire
Juveniles with a finely denticulate margin	Juveniles with a nearly smooth margin
Concentric grooving on carapace shields weak or absent	Concentric grooving on carapace shields usually strong
Posterior angle of gular scutes well forward of the entoplastron	Posterior angle of gular scutes encroaching on the entoplastron
Dorsal surface of each gular scute usually divided (=4 dorsal gulars)	Dorsal surface of each gular scute usually undivided (=2 dorsal gulars)
Humeral median suture usually longer than femoral median suture	Femoral median suture usually longer than humeral median suture
Inguinal narrowly in contact with femoral on ventral plane of plastron, i.e. inconspicuous in ventral view	Inguinal broadly in contact with femoral on ventral plane of plastron, i.e., conspicuous in ventral view

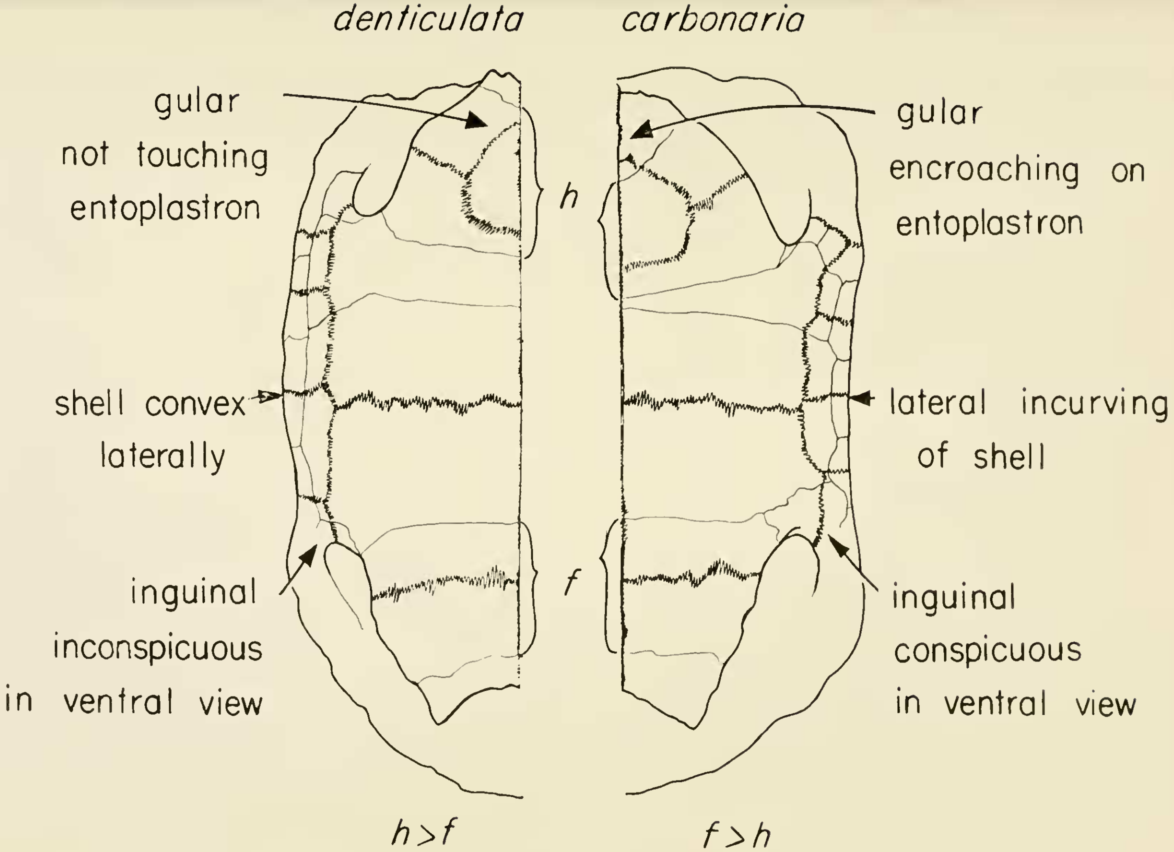

Fig. 1. Plastra of *G. denticulata* and *G. carbonaria* compared. *h*, humeral; *f*, femoral.

Each of these characters shows variation and therefore requires comment:

Color. The color of the carapace is very strikingly distinct in most specimens of the two species, and, so far as I know, is invariably diagnostic in juveniles. However, a few of the older *denticulata* may show a strongly contrasting pattern of orange and dark brown not unlike the black and yellow of *carbonaria;* the colors, however, are duller and the light areolae wider and less sharply bounded.

Prefrontal and frontal scales. These differences will hold in most specimens but not in all. Some tendency to a break-up of the frontal occurs in a few *carbonaria;* while the converse tendency to a nearly entire frontal is present in some *denticulata.*

Denticulate margin in juveniles. This is a very consistent character in spite of the fact that, examined under magnification, hatchlings of *carbonaria* show faint traces of the denticulations so characteristic of its sibling.

Concentric grooving of carapace shields. A character often but not invariably useful.

Gular scutes encroaching on entoplastron or not. So far as it has been possible to check, a consistent character.

Dorsal surfaces of gular scutes subdivided or not. Only statistically useful.

Humeral/femoral ratio. Usually a very good character, but a few *carbonaria* have the femoral and humeral subequal.

Inguinal-femoral relationship. An excellent diagnostic character if attention is paid to the precise relationship. In both *carbonaria* and *denticulata* the inguinal scute is rather triangular, not narrowed anteroposteriorly as in the two other species of neotropical tortoises, *chilensis* and *elephantopus.* In *denticulata*, however, the scute is smaller than in *carbonaria* and not at all conspicuous in direct ventral view. There may be in *denticulata* a relatively broad contact with the femoral but this is on the edge of the plastron at the inguinal, not as in *carbonaria* on the main ventral plane of the plastron. To see the inguinal-femoral contact clearly in *denticulata* it is necessary to turn the animal to the side to examine the plastral edge. In *carbonaria* the broad contact of inguinal and femoral is best seen in straight ventral view.

Two characters not tabulated may be significant:

1. *Size.* Specimens of *denticulata* from eastern Peru (Bassler collection, American Museum) are the largest South American tortoises I have seen. AMNH 58084 has a carapace length of 673 mm. and AMNH 58085 is but little smaller (637 mm.). No *carbonaria* approach this size, though both species of northern South America are larger than *chilensis*, the third species in southern South America.

2. *Carapace shape.* Both species tend to have parallel-sided shells. However, *carbonaria* appear on the average to have narrower shells, often in fact indented midlaterally to give a dumbbell shape in dorsal view. *Denticulata* may have more rounded contours. There is, however, much variability.

Many of the South American tortoises in collections have no or very poor data. It is therefore difficult to get a precise idea of the geographic relationships of the two species. I list below in parallel columns the most precise localities that I have been able to obtain for specimens examined by me.

denticulata	*carbonaria*
Colombia	**Colombia**
....	*Dept. Atlantico:* Cienega de Guajaro Puerto Bello
....	*Dept. Antioguia:* Golfo de Urabá
Dept. Caquetá: S. of Florencia Morelia	....
....	*Dept. Cundinamarca:* W. of Honda
....	*Dept. Magdalena:* Rio Frio Totumal
Dept. Meta: Villavicencio	....
Venezuela	**Venezuela**
....	*Barinas State:* Barinas

denticulata (cont.)	*carbonaria* (cont.)
. . . .	*Carabobo State:*
	Maracay
Monagas State:	. . . .
Juanipa River near Caripito	
Territorio do Amazonas:	. . . .
foothills Mt. Dueda	
	no state:
	Orinoco Region
	Rio Apure
	Los Testigos
Trinidad	. . . .
British Guiana	**British Guiana**
Demerara	Essequibo River nr. Onara
	(70 miles from Georgetown)
Essequibo River	
Kamakusa	Kamakusa
Kartabo	head of Rupononi River
Oho Mtn.	
Surinam	**Surinam**
"Paramaribo"	Cottica
French Guiana	. . . .
"Cayenne"	
Peru	. . . .
Dept. Junin:	
Atalaya	
Dept. Loreto:	
Alto Rio Pisqui	
Iquitos	
Pucallpa	
Rio Ucayali	
Rio Napo	
Yarinacocha	
Brasil	**Brasil**
Amazonas State:	*Amazonas State:*
Lago Aleixo (Thayer Exped.)	Manaus
Lago Januarí (Thayer Exped.)	Villa Bella (Thayer Exped.)
Manaus	
Rio Negro	

denticulata (cont.)	*carbonaria* (cont.)
Rio Jurua	
Tefé	
Para State:	*Para State:*
Belem (= "Pará")	Belem (="Pará")
Fordlandia	Fordlandia
	São Mateus
Maranhão State:	*Maranhão State:*
Chatão, Rio Gurupi	Barra do Corda, Rio Mearim
Goiás State:	*Goiás State:*
Anapolis	Barra do Rio São Domingo
	Cana Brava
....	*Mato Grosso State:*
	Maracuju
	Miranda
	Nioac
Espiritu Santo State:	....
Rio Doce	
....	*Rio Branca Prov.:*
	between Frechal and Limao on Rio Surumú
....	*Distrito Federal:*
	Recreio de Bandeirantes, S. of Rio de Janeiro
state unknown	
Fia (W. James—Thayer Exped.)	
Xeberos (Brit. Mus.—purch. Higgins)	
Bolivia	**Bolivia**
....	*Dept. Chaco:*
Dept. Pando:	....
Baracca, Rio Madidi	
Dept. Santa Cruz:	*Dept. Santa Cruz:*
Fortin Cañada Larga	San Jose de Chiquitos
....	**Paraguay**
	Asuncion
	Rio Paraguay
	Ybabopo

It is easily seen that the localities, more restricted than state or department, from which both species are currently recorded, are few. Even in these cases it is doubtful whether the two species have been taken together in any literal sense: it may well be that these place names are merely central points for large collecting areas.

However, the localities for the two forms are so interwoven and the forms themselves so distinct that any interpretation except that of species distinction appears difficult. In any event, the biological situation is an extremely interesting one, and it would be worthwhile to have precise information on their habitats and habits. No detailed information of this sort is at present available. Dr. P. E. Vanzolini comments on the Brasilian localities as follows:

"Some are in deep forest, some in the cerrado. I have collected the beast in the cerrado area (Barra do Corda), but it was in small wooded spots or gallery forests. Our eastern Goiás specimens are in the same case — in the Blaser collection are several typical forest forms. I flew over the area on purpose and found out that there are quite extensive wooded areas.

Localities in undoubtedly forested areas: All in Amazonas and Pará, Chatão, Rio Doce, Recreio dos Bandeirantes.

Localities where I know there is for sure at least gallery forest: Every single other!

Incidentally, in Maranhão (Barra do Corda) several of my specimens were caught in dens (terribly damp and muddy) but not by myself. The habit is known by all *there*."

It is interesting that in eastern Peru only *denticulata* is known. This was reported already by Sclater in 1871 (p. 744) from observations by E. Bartlett. The situation in Amazonian Colombia appears similar. By contrast, only *carbonaria* is known from northern Colombia, Paraguay and southern Brasil (Rio de Janeiro).

I have thus far used the names *denticulata* and *carbonaria* without justifying this procedure. A few comments on the nomenclature are required.

Testudo denticulata was described by Linnaeus in the 12th edition of the *Systema Natura* (1766) on the basis of a specimen in the Museum de Geer. The brief description would not suffice for identification if Schoepff had not published in 1792 a figure of a specimen which may well be the one cited by Linnaeus. According to Schoepff (p. 140), the Museum de Geer had had not one but two specimens, one of which, at the time of Schoepff's writing, was located in Stockholm and the other in Upsala. The latter specimen is that figured by Schoepff (in color, in some editions). Schoepff compares this specimen carefully with Linnaeus' description and considers it to be Linnaeus' type; Andersson (1900), re-examining the specimen, has agreed with Schoepff.

Schoepff's figure (plate 28), in spite of a certain crudity, is unquestionably the species here called *denticulata*. The denticulations that gave the species its name are clearly shown and the colored editions show the characteristic yellow brown of juveniles of this species. Thus there can be no doubt about the name of this form.

The next name proposed was *Testudo tabulata* Walbaum 1782. No figure exists, but the description of the color of the shell as "castaneo et sulphureo" in the Latin text (p. 122), or "castanien brauner und hellgelber Farbe" in the German text (p. 75), sufficiently identifies this as the brown form and thus a synonym of *denticulata* Linnaeus.

Testudo tessellata Schneider 1792 is the next name available. It is, however, a composite, based partly on an older description which has always been cited in the synonymy of *carbonaria* and partly on a description and figure which as clearly apply to *denticulata*. Schneider's detailed description is taken from the figure and it is best to assign his proposed name to this concept and thus to the synonymy of *denticulata*.

Four names were proposed by Spix (1824), all illustrated by adequate figures. Three — *hercules*, *sculpta*, and *cagado* — are clearly differing sizes and minor color varieties of the brown tortoise of northern South America. The fourth — *carbonaria* — is clearly the black and yellow species of this paper.

The adjoining plates of *sculpta* and *carbonaria* show, in addition to the difference in coloration (here at its most extreme because an essentially unicolor young *denticulata* is pictured), the characteristic differences in humeral-femoral ratio and in the relation of inguinal to femoral. *Carbonaria* Spix is unmistakably the name to be applied to the second species in northern South America.

T. boiei Wagler 1833 is a later name and cannot disturb the nomenclature here adopted. Wagler's plate clearly identifies his species as *carbonaria*. Once again the black and yellow of the dorsal shell is well shown and on the plastron the diagnostic humeral-femoral ratio and inguinal pattern.

Other Neotropical Species

The tortoises of South America and the Galapagos form a natural group for which the subgenus *Chelonoidis* of the genus *Geochelone*[1] may be employed. There are four living species:

Geochelone denticulata Linnaeus, *G. carbonaria* Spix, *G. chilensis* Gray, *G. elephantopus* Harlan.

The following key will aid in the separation of these species:

1. Dorsal color uniform brown or black, or brown with vaguely bounded orange areolae. Humeral median suture longer than femoral 2
Dorsal color black and yellow, the areolae bright yellow sharply delineated. Femoral median suture longer than humeral.
G. carbonaria Spix.
Northern South America south to Paraguay and
Rio de Janeiro but not Amazonian Peru.

2. Inguinal *narrow* anteroposteriorly with a conspicuous contact with the femoral. Shell rounded elliptical in adults, not denticulate in hatchlings 3
Inguinal smaller, more triangular, not conspicuously in contact with femoral in straight ventral view. Shell elongate elliptical in adults, denticulate in hatchlings. *G. denticulata* Linnaeus.
Northern South America except northern Colombia,
south to Bolivia but not Paraguay, and to Espiritu
Santo but not Rio de Janeiro.

3. Size small (to 220 mm.). Gular region bifid, shell margin subserrate.
G. chilensis Gray.
Paraguay, S. Brasil and N. Argentina.
Size giant (to more than 1 m.). Gular region truncate, shell margin entire. *G. elephantopus* Harlan.
Galapagos Islands.

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[1] For the use of *Geochelone* rather than *Testudo* see Loveridge and Williams, 1957, pp. 211-219.

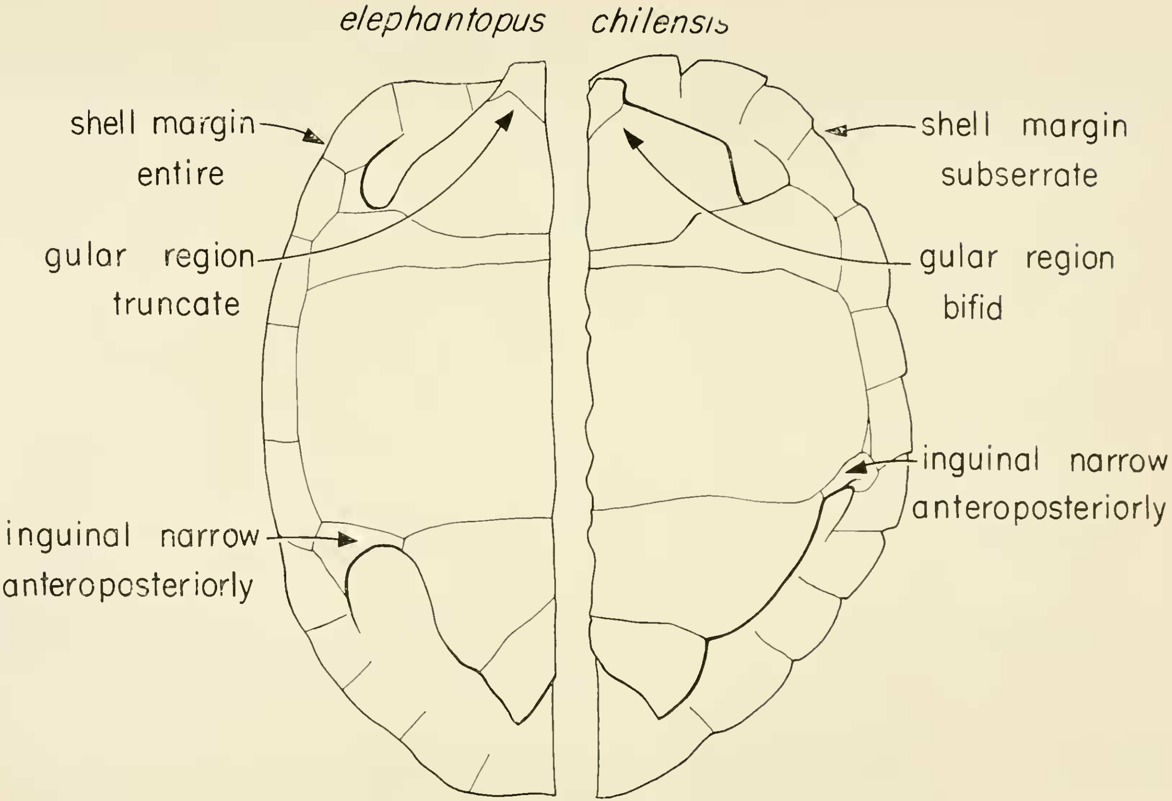

Fig. 2. Plastra of *G. elephantopus* and *G. chilensis* compared.

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